

REVIEW AND SYNTHESIS

Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations

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Abstract

Fitness costs of reproduction play a key role in understanding the evolution of reproductive tactics. Nevertheless, the detection and the intensity of costs of reproduction vary according to which life-history traits and species are studied. We propose an evolutionary model demonstrating that the chance of detecting a cost of reproduction should be lower when the fitness component studied has a low rather than high variance. Consequently, the fitness component that is affected the most by costs of reproduction should vary with life speed. Since long-lived species have developed a strategy that avoids jeopardizing their survival and short-lived species favour current reproduction, variance in survival is smaller and variance in reproduction higher in long-lived vs. short-lived species. We review empirical studies of costs of reproduction in free-ranging mammals, comparing evidence of costs reported among species and focal traits. In support of our model, more studies reported evidence of reproductive costs of reproduction in ungulates than in rodents, whereas survival costs of reproduction were more frequent in rodents than in ungulates. The life-history model we propose is expected to apply to any species, and hence provides a better understanding of life-history variation, which should be relevant to all evolutionary ecologists.

Keywords

Environmental canalization, investment, mammals, reproductive tactics, resource acquisition, resource allocation, rodents, ungulates, van Noordwijk and de Jong's model, variable environment.

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Positive or negative co-variations among fitness components are central to life-history theory (Stearns 1992). The notion of negative co-variations originates from the principle of allocation (Williams 1966), which posits that resources available for an individual are limited, so that individuals should allocate resources optimally among growth, survival, and reproduction in order to maximize their fitness (Stearns 1992). As reproduction requires high energy allocation (Robbins 1993), fitness costs of reproduction (see Box 1 for definitions) should occur and lead to negative co-variations between current reproduction and future survival and/or reproduction (Stearns 1992; Roff 2002). Williams (1966) was the first to introduce this cost-benefit concept of reproduction, which was further developed by numerous authors (e.g. Gadgil & Bossert 1970; Bell 1980; Reznick *et al.* 2000). Costs of reproduction have received a particular attention in

the literature because they play a key role in the evolution of reproductive tactics (Roff 2002). They can also have fundamental demographic consequences on population dynamics by decreasing reproduction and survival, and thereby changing the population age structure and growth rate (Silvertown & Dodd 1999; Proaktor *et al.* 2008).

As energy allocation is particularly important during gestation and lactation (Gittleman & Thompson 1988), mammals are relevant model species to assess costs of reproduction. In his review of studies on life-history, Stearns (1992) reported only six studies on non-domestic populations of mammals of 179 studies across all taxa that reported on costs of reproduction. This lack of research on costs of reproduction in free-ranging mammals up to that time was likely due to the scarcity of longitudinal studies of marked individuals. Since then, analyses of mammalian populations

have greatly improved (see Tables 1 and 2), permitting a new comparative review on costs of reproduction in different mammalian groups.

Box 1 The notion of costs of reproduction – essential definitions

Despite several attempts to provide a clear definition of *parental investment* in an evolutionary context, *parental investment* is repeatedly misused in the literature, being confused with *parental care* and *reproductive expenditure* (see e.g. Mendl & Paul 1989; Derocher & Stirling 1998). Concomitantly, the expression ‘costs of reproduction’ is repeatedly misused in the literature. Here, we clarify some essential definitions (see also Appendix S1 for a discussion on how costs of reproduction should be measured).

Parental care (or parental allocation): encompasses any behaviour provided to the offspring by the parents and should be used as long as a direct relationship between parent’s future fitness and the observed *parental care* has not been demonstrated (Evans 1990; Clutton-Brock 1991).

Reproductive expenditure (or reproductive allocation): quantifies the amount of energy allocated to reproduction, and as for *parental care*, it makes no assumption on whether or not it incurs fitness costs to the parent.

Parental investment: only includes *parental care* (allocation) and/or *reproductive expenditure* (allocation) that entail fitness costs following reproduction, i.e. decreasing the future survival or reproductive success of the parent while improving offspring’s fitness (Trivers 1972).

Energetic costs of reproduction: short-term costs generated from physiological changes as a result of reproductive effort, i.e. *parental care* (allocation) and *reproductive expenditure* (allocation) (Speakman 2008).

Fitness costs of reproduction: long-term costs resulting from *parental investment* (Clutton-Brock 1991; see Appendix S1 for details on how fitness costs of reproduction should be measured).

Indirect costs of reproduction: costs resulting from *parental investment* that do not directly influence fitness components, but influence other traits (e.g. parturition date, offspring mass, energy reserves or body growth of females for the next reproductive attempts) that in turn decrease juvenile survival or future reproductive performance. When variations in traits other than reproduction or survival at $t + 1$ results from reproduction at time t , they should only be considered as costs of reproduction if a link is demonstrated between these variations and the residual reproductive value of the individual reproducing at time t (see Appendix S2 for examples on how to measure these costs).

The objectives of this review were to (1) clarify and redefine the theoretical background that could explain why the occurrence and intensity of fitness costs of reproduction vary among species and traits and (2) update and summarize empirical evidence of fitness costs of reproduction collected in non-domestic mammalian populations. We thus propose an evolutionary model to explain patterns of variation in costs of reproduction, based on variation in fitness components, and assess its validity using empirical evidence of costs of reproduction published from mammalian populations. We subsequently discuss the challenges in assessing costs of reproduction and illustrate the potential statistical pitfalls and confounding factors to be considered in these studies. Finally, we conclude by identifying areas for future research based on the empirical patterns emerging from our review.

WHEN SHOULD WE EXPECT TO FIND COSTS OF REPRODUCTION?

Influence of variance in resource acquisition and allocation among individuals within a population

In their seminal work, van Noordwijk & de Jong (1986) proposed a model to explain why positive or negative correlations had been observed from empirical analyses of current reproduction vs. future survival or reproduction. Their model was based on the relative variation in resource acquisition vs. allocation among individuals resulting from genotypic and/or phenotypic variations. In their model (Fig. 1A), the three isoclines ‘ a ’ represent the total amount of resources available to allocate between two competing functions (here current reproduction and future survival) for three hypothetical individuals. The individual following the isocline ‘ $a = 3$ ’ has three times more resources available than the individual that follows the isocline ‘ $a = 1$ ’. Variance in ‘ a ’ therefore corresponds to individual variation in resource acquisition within a population. Individual heterogeneity in resource acquisition may arise from variation in age (MacNulty *et al.* 2009a), body mass (MacNulty *et al.* 2009b), and home range quality (McLoughlin *et al.* 2007), or as a result of variation in environmental conditions (e.g. density, climate; Hamel *et al.* 2009a). Furthermore, the strategy of resource allocation may also vary among individuals (Moyes *et al.* 2009). The extreme opposite strategies occur at each end of the isoclines, where all resources are allocated either to current reproduction (where the isoclines meet the x -axis) or to survival (where they meet the y -axis). In Fig. 1A, three strategies of resource allocation for three different individuals are presented: one individual allocates most resources to survival ($b = 0.75$), one allocates equally between survival and current reproduction ($b = 0.50$), and one allocates mostly to current reproduc-

Table 1 Summary of mammalian studies on costs of reproduction in terms of survival, where current reproduction (‘trait at time t ’) was distinguished in two reproductive life stages: costs associated with parturition ‘Birth’, and with weaning success ‘Success’. No study assessed survival costs in relation with conception

Population no. and species	Study location	Trait (time t)	Cost ¹	Effect size ²	D ³	N ⁴	Scale ⁵	M ⁶	C ⁷	Method used ⁸	References ⁹
Rodents											
1 Bank vole <i>Clethrionomys glareolus</i>	Konnevesi, Finland	Success	Y	~0.20 - 0.25	-	94	R,C vs. E	Y	E	GLM	1
2 Bank vole <i>Clethrionomys glareolus</i>	Konnevesi, Finland	Success	N	~0.12	+	10; 23	R,C vs. E	Y		χ^2	2,3
3 Bank vole <i>Clethrionomys glareolus</i>	Konnevesi, Finland	Birth	Y ^(a)	0.27	-	16; 19	C vs. E	Y		GLM	4
4 Bank vole <i>Clethrionomys glareolus</i>	Konnevesi, Finland	Birth	Y ^(b)	~0.20	-	151	0 vs. 1	Y	IE	GLMM	5
5 Banner-tailed kangaroo rat <i>Dipodomys spectabilis</i>	Portal, USA	Birth	N	0.04	+	419; 85	0 vs. 1**	N	IE	GLM	6
6 Banner-tailed kangaroo rat <i>Dipodomys spectabilis</i>	Rucker, USA	Success	N	0.02	+	398; 95	0 vs. 1**	N	IE	GLM	6
7 Black-tailed prairie dog <i>Cynomys ludovicianus</i>	Wind Cave National Park, USA	Birth	N	0.13	-	121; 24	0 vs. 1**	N	IE	GLM	6
8 Columbian ground squirrel <i>Spermophilus columbianus</i>	Sheep River, Canada	Success	N	~0.07	+	339; 399	0 vs. 1	N	I	χ^2	7
9 Columbian ground squirrel <i>Spermophilus columbianus</i>	Dyson Creek, Canada	Birth	Y ^(c)	~0.50	-	13; 26	2,3 vs. 4***	N	IE	χ^2	9
10 Columbian ground squirrel <i>Spermophilus columbianus</i>	George Creek, Canada	Success	N ^(d)	0.04	+	58; 16	0 vs. 1	N		G test	10
11 Columbian ground squirrel <i>Spermophilus columbianus</i>	Highwood Pass, Canada	Birth	N	N/A	N/A	N/A	N/A	N		G test	10
12 Columbian ground squirrel <i>Spermophilus columbianus</i>	Sheep River, Canada	Success	Y	0.17	-	74; 33	0 vs. 1	N		G test	10
13 Columbian ground squirrel <i>Spermophilus columbianus</i>	Sheep River, Canada	Birth	N	N/A	N/A	N/A	N/A	N		G test	10
14 Columbian ground squirrel <i>Spermophilus columbianus</i>	Turnbull National Wildlife Refuge, USA	Success	N	0.06	+	67; 61	0 vs. 1	N		G test	10
15 Deer mouse <i>Peromyscus columbianus</i>	Kananaskis Valley, Canada	Success	Y	0.08	-	230; 115	0 vs. 1**	N		χ^2	11
16 European ground squirrel <i>Spermophilus citellus</i>	Recreational park in Vienna	Success	Y	0.19	-	148; 58	0 vs. 1	N		χ^2	11,12
		Success	N ^(e)	0.20	+	41; 38	0 vs. 1	N		χ^2	13
		Success	N	N/A	N/A	N/A	N/A	N		χ^2	14
		Success	N	0.05	-	96	0 to 7	N		GLM	15
		Birth	N	0.08	-	40	3 to 10	N	I	GLM	16

Table 1 continued

Population no. and species	Study location	Trait (time t)	Cost ¹	Effect size ²	D ³	N ⁴	Scale ⁵	M ⁶	C ⁷	Method used ⁸	References ⁹
17 Meadow vole <i>Microtus pennsylvanicus</i>	Patuxent Wildlife Research Center, USA	Birth	N	0; 0.17	+	N/A	0 vs. 1	N	E	MCMR*	17
18 Meadow vole <i>Microtus pennsylvanicus</i>	4 populations in Wisconsin, USA	Birth	Y	N/A	-	52; 51	0 vs. 1	Y	I	N/A	18
19 North American red squirrel <i>Tamiasciurus hudsonicus</i>	Kluane National Park, Canada	Birth	Y ^(f)	0.06	-	143; 170	0 vs. 1	N	E	GLM	19
20 Richardson's ground squirrel <i>Spermophilus richardsonii</i>	Picture Butte, Canada	Success	Y ^(g)	0.11; 0.55	-	453; 393	0 vs. 1**	N	IE	GLMM	20
21 Richardson's ground squirrel <i>Spermophilus richardsonii</i>	Picture Butte, Canada	Birth	N	N/A	N/A	999	1 to 13***	N	GLM	GLM	21
22 Townsend's vole <i>Microtus townsendii</i>	Vancouver, Canada	Success	N	0.14	-	233; 16	0 vs. 1**	N		χ^2	22
23 Bighorn sheep <i>Ovis canadensis</i>	Ram Mountain, Canada	Birth	Y ^(h)	~0.20	-	233	5 to 8	N	IE	GLM	23
24 Bighorn sheep <i>Ovis canadensis</i>	Sheep River, Canada	Success	N	N/A	N/A	142 (ID)	0 vs. 1	N	IE	GLM	24
25 Moose <i>Alces alces</i>	Nelchina Basin, Alaska	Success	N	0.02	-	447 (ID)	0 vs. 1	N	IE	GLM	24
26 Mountain goat <i>Oreamnos americanus</i>	Caw Ridge, Canada	Success	N	0.00	=	555	0 vs. 1	N	IE	GEE*	27
27 Red deer <i>Cervus elaphus</i>	Isle of Rum, Scotland	Birth	Y ⁽ⁱ⁾	N/A	-	555	0 vs. 1	N	IE	GEE*	27
28 Reindeer <i>Rangifer tarandus</i>	Kaamanen, Research Station, Finland	Success	N	~0.03 - 0.30	-	529 (ID)	0 vs. 1	N	IE	CMR*	28
29 Soay sheep <i>Ovis aries</i>	Village Bay area, Hirta Island, Scotland	Birth	Y ^(k)	~0.10 - 0.30	-	328; 290	0 vs. 1	N	IE	GLM	29,30
Others						N/A	0 vs. 1	N	I	MCMR*	31
30 Antarctic fur seal <i>Arctocephalus gazella</i>	Bird Island, South Georgia	Birth	Y ^(l)	0.08	-	1173; 420	0 vs. 1	N	IE	CMR/GLM	31
31 Common marmoset <i>Callithrix jacchus</i>	National Zoological Park, USA	Success	Y ^(m)	0.64	-	11; 6	1 to 2	N	I	χ^2	36
32 European badger <i>Meles meles</i>	Myrtham Woods, UK	Birth	Y ^(h)	0.13; 0.32	-	50; 38	0 vs. 1	N	I	χ^2	37

Table 1 continued

Population no. and species	Study location	Trait (time <i>t</i>)	Cost ¹	Effect size ²	D ³	N ⁴	Scale ⁵	M ⁶	C ⁷	Method used ⁸	References ⁹
33 Fur seal <i>Arctophthalmus tropicalis</i>	Amsterdam Island, Indian Ocean	Birth	N	0; 0.18	+	238 (ID)	0 vs. 1	N	IE	MCMR*	38
34 Lion <i>Panthera leo</i>	Serengeti National Park, Tanzania	Birth	N	N/A	+	3310	0 vs. 1	N		GLM	39
35 Olive baboon <i>Papio anubis</i>	Gombe National Park, Tanzania	Birth	N	N/A	+	1518	0 vs. 1	N		GLM	39
36 Southern elephant seal <i>Mirounga leonina</i>	Marion Island, Indian Ocean	Birth	Y ⁽ⁿ⁾	0.08	-	861 (ID)	0 vs. 1	N	E	CMR*	40
37 Weddell seal <i>Leptonychotes weddellii</i>	Erebus Bay, Antarctica	Birth	Y	0.04	-	607 (ID)	0 vs. 1	N	IE	MCMR*	41
38 Weddell seal <i>Leptonychotes weddellii</i>	Vestfold Hills, Antarctica	Birth	N	0.00	=	1368 (ID)	0 vs. 1	N	E	MCMR*	42

Notes: We reviewed the primary literature using the ISI Web of Knowledge database (Thompson Reuters) to compile published studies on costs of reproduction in mammals. Our main search included studies published until September 2009 and was based on a combination of two keywords, 'cost/costs' and 'reproduction/reproductive'. Although this search was very wide, we did not restrict it with other keywords because it excluded papers on costs of reproduction. Instead, we excluded journals publishing studies specific to plants, fish, birds, reptiles, amphibians, invertebrates, economy, medicine and humans. We also performed a specific search to include studies that contained any of the following keywords 'primiparity', 'primipare', 'primiparous', 'birth interval' or 'interbirth interval', again excluding journals mentioned above. We also included in our review relevant studies presented in Stearns (1992). We did not perform an intensive search in scientific books, but we included results from books for which we knew costs of reproduction had been presented and not published in the primary literature. The information we reported is for each population studied, considering studies from the same location to be different populations if they were performed in different years. When more than one study reported costs for the same population, we retained the most recent study. In cases where effect sizes were not directly provided in the paper, we either estimated the effect from figures or averaged them if effects were provided for different categories (e.g. averaging effect across age classes). N/A, information not available or data not in a comparable format.

¹Y, costs of reproduction reported; N, no cost reported; (a), only a tendency; (b), costs only for lighter females; (c), costs only during crash years; (d), not studied during crash years; (e), only studied 2 years old females; (f), only studied primiparous females; (g), costs only in young and old females; (h), costs only in young females; (i), costs only in old females; (j), costs mainly in young and old females and in years of low food availability; (k), costs only in crash years and for older/younger females, and stronger effect for lighter females; (l), stronger effects for younger primiparous; (m), costs only in small females; (n), only studied primiparous vs. multiparous females, stronger effect during crash years.

²Effect sizes that were estimated from figures or from different categories (see Notes) are marked with '~'.

³D, direction of the effect.

⁴N, sample size in terms of female-events; ID, the number of female-events was not available, so the sample size provided represents the number of females included in the study. When available, sample size was separated in different female categories and presented in the following order: reproductive vs. non-reproductive females, or females with large vs. small litter size.

⁵Scale on which the effect size is based upon, where numbers represent the number of offspring; R, reduced litter; C, controlled litter; E, enlarged litter; **no effect of different litter size on survival; ***no effect of 0 vs. 1.

⁶M, experimental manipulation of reproductive effort; Y, yes; N, no.

⁷C, (co)variables included in the analyses; I, study accounted for variable(s) relating to individual quality; E, study accounted for variable(s) relating to environmental conditions.

⁸GLM, generalized linear model; GLMM, generalized estimating equations model; GEE, generalized estimating equations model; CMR, capture-mark-recapture model; MCMR, multistate capture-mark-recapture model; *studies that used an information-theoretic approach (e.g. Akaike Information Criterion).

⁹References are provided in Appendix S3.

tion ($b = 0.25$). Variance in ' b ' therefore represents the relative among-individual variation in resource allocation strategy.

Based on their model, van Noordwijk & de Jong (1986) demonstrated that when the relative variation in resource acquisition is larger than the relative variation in resource allocation among individuals, a positive correlation should be observed between current reproduction and future performance at the population scale (Fig. 1B). In that case, variation in individual quality (*sensu* Wilson & Nussey 2010) resulting from variation in resource acquisition could mask the fitness costs of reproduction that are theoretically expected. Costs of reproduction should instead be apparent in the opposite case, when the among-individual variation in resource acquisition is smaller than the among-individual variation in resource allocation (Fig. 1C). In support of van Noordwijk & de Jong's model, studies accounting for some level of heterogeneity among individuals reported evidence of costs of reproduction more frequently than studies that did not (see 'Confounding variables and statistical issues' section). However, even after controlling for individual heterogeneities, many studies reported costs of reproduction only in specific traits, while there was no evidence that other traits were affected by current reproduction. In bighorn sheep (*Ovis canadensis*), for example, costs of reproduction in terms of probability of weaning a future offspring occurred mainly in females with low body mass and at high population density (Festa-Bianchet *et al.* 1998). However, even after accounting for individual quality and density, no survival cost of reproduction was detected (Festa-Bianchet *et al.* 1998). Hence, although the acquisition and allocation model of van Noordwijk & de Jong (1986) has shown to be of tremendous help in untangling the existence of costs of reproduction, patterns in the occurrence and intensity of these costs across species and traits remain unexplained.

Influence of variance in life-history traits

One fundamental aspect that was not included in the van Noordwijk & de Jong's model is the variance in fitness components themselves. The variance observed in fitness components is the result of both a statistical and a biological influence. Statistically, the relationship between the mean and the variance of binomially distributed traits (i.e. proportions; as the mean approaches 0 or 1, the variance is constrained to 0) will result in fitness traits with mean close to 1 to have smaller variance than traits with mean close to 0.5 (Gaillard & Yoccoz 2003). Biologically, the variance observed in fitness components is also constrained as a result of environmental canalization (Stearns *et al.* 1995; Gaillard & Yoccoz 2003). Indeed, for a given species, and thereby within a broad type of reproductive tactics, the response to a given change in environmental conditions

strongly varies among fitness components (e.g. Stearns *et al.* 1995; Pfister 1998; Gaillard *et al.* 2000; Morris & Doak 2004). Long-lived species have evolved a slow life-history strategy, involving a conservative reproductive tactic. Individuals favour their own survival over that of their offspring because longevity is the key to obtain a greater fitness (Clutton-Brock 1988; Newton 1989). Hence, survival shows low variance within a range of conditions as a result of environmental canalization, both on an absolute scale and relative to its mean (Gaillard & Yoccoz 2003), whereas reproduction is more variable (Gaillard *et al.* 1998). Conversely, short-lived species have evolved a fast life-history strategy. Individuals allocate a high reproductive effort at each of their few reproductive occasions (Speakman 2008). Consequently, environmental canalization has led to low variance in reproduction while survival is highly variable, both on an absolute scale and relative to its mean (Gaillard & Yoccoz 2003).

If the biological influence of environmental canalization that constrains variance of fitness components is included in the model of van Noordwijk & de Jong (where costs of reproduction are expected to be detected, i.e. Fig. 1C), we can see that the zone where the observations are lying is small and shows no cost of reproduction when survival has low variance (Fig. 1E), whereas this zone is large and shows a cost when survival has high variance (Fig. 1D). This demonstrates that the chance of finding evidence of costs of reproduction should be lower when the fitness component investigated has a low compared with a high variance.

To generalize van Noordwijk & de Jong's model to include the biological influence of environmental canalization constraining the variance in fitness components, we analysed demographic patterns of females between two mammalian groups: rodents and ungulates. These two groups are ideal for this demonstration because they have contrasting life-history strategies where rodents show lower variance in reproduction and higher variance in survival compared with ungulates (Gaillard & Yoccoz 2003). In addition, costs of reproduction have been studied more frequently in rodents and ungulates than in other mammalian groups (see Tables 1 and 2), therefore making it possible to test our model by reviewing the empirical support published from these two groups. Based on the different patterns of variance in fitness components between rodents and ungulates (Gaillard & Yoccoz 2003), we illustrated the potential for observing costs of reproduction in terms of survival and future reproduction in these species (Fig. 2). In all cases, we kept the relative variance in resource acquisition constant at 0.2 and that of resource allocation at 0.4, to represent a situation where costs of reproduction are expected (van Noordwijk & de Jong 1986; Fig. 1C). Although the exact locations of the curves are not particularly important, we placed the relative resource

Table 2 Summary of mammalian studies on costs of reproduction in terms of future reproduction, where future reproduction ('trait at time $t + 1$ ') was divided in six categories (probability of conceiving 'Conception', litter size at conception 'LS conception', probability of parturition 'Birth', litter size at parturition 'LS birth', probability of weaning offspring 'Success', litter size at weaning 'LS success') and current reproduction ('trait at time t ') was distinguished in three reproductive life stages (costs associated with conception 'Conception', with parturition 'Birth' and with weaning success 'Success')

Population no. and species	Study location	Trait (time t)	Trait (time $t + 1$)	Cost ¹	Effect size ²	D ³	N ⁴	Scale ⁵	M ⁶	C ⁷	Method used ⁸	References ⁹
Rodents												
1 Alpine marmot <i>Marmota marmota</i>	Berchtesgaden National Park, Germany	Success	Birth	Y	0.14	-	110; 81	0 vs. 1+	N		χ^2	43
2 Bank vole <i>Clethrionomys glareolus</i>	Konnevesi, Finland	Success	Birth	N	~0.08	+	103	R,C vs. E	Y	E	GLM	1
3 Bank vole <i>Clethrionomys glareolus</i>	Konnevesi, Finland	Success	LS birth	Y ^(a)	0.6	-	103	R,C vs. E	Y	E	ANOVA	1
4 Bank vole <i>Clethrionomys glareolus</i>	Konnevesi, Finland	Success	Birth	N	~0.13	-	24; 24	C vs. E	Y	E	GLM	44
5 Bank vole <i>Clethrionomys glareolus</i>	Konnevesi, Finland	Success	LS birth	N	~0.9	+	24; 24	C vs. E	Y	E	ANOVA	44
6 Bank vole <i>Clethrionomys glareolus</i>	Konnevesi, Finland	Success	Birth	N	N/A	+	54	C vs. E	Y	E	GLM	45
7 Bank vole <i>Clethrionomys glareolus</i>	Konnevesi, Finland	Success	LS birth	N	N/A	N/A	54	C vs. E	Y	E	ANOVA	45
8 Bank vole <i>Clethrionomys glareolus</i>	Konnevesi, Finland	Success	Birth	N	N/A	N/A	72	C vs. E	Y	I	GLMM	46
9 Bank vole <i>Clethrionomys glareolus</i>	Konnevesi, Finland	Success	LS birth	N	N/A	N/A	72	C vs. E	Y	I	GLMM	46
10 Black-tailed prairie dog rats <i>Cynomys ludovicianus</i>	Konnevesi, Finland	Success	Birth	N	~0.18	-	12; 22	R,C vs. E	Y		χ^2	3
11 Canadian beaver <i>Castor canadensis</i>	Portail, USA	Success	LS birth	N	~0.5	+	7; 17	R,C vs. E	Y		χ^2	3
12 Columbian ground squirrel <i>Spermophilus columbianus</i>	Portail, USA	Success	LS success	N	~1.3	+	7; 17	R,C vs. E	Y		χ^2	3
13 Columbian ground squirrel <i>Spermophilus columbianus</i>	Konnevesi, Finland	Birth	Birth	Y ^(b)	N/A	-	10; 17	C vs. E	Y	I	GLM	4
14 Banner-tailed kangaroo rat <i>Dipodomys spectabilis</i>	Finland	Birth	LS birth	N	N/A	N/A	317 (ID)	0 to 6	N	IE	GLM	6
15 Banner-tailed kangaroo rat <i>Dipodomys spectabilis</i>	Portail, USA	Success	LS birth	N	N/A	N/A	317 (ID)	0 to 6	N	IE	GLM	6
16 Banner-tailed kangaroo rat <i>Dipodomys spectabilis</i>	Rucker, USA	Success	LS birth	N	N/A	N/A	101 (ID)	0 to 6	N	IE	GLM	6
17 Black-tailed prairie dog rats <i>Cynomys ludovicianus</i>	Rucker, USA	Success	LS birth	N	N/A	N/A	101 (ID)	0 to 6	N	IE	GLM	6
18 Black-tailed prairie dog rats <i>Cynomys ludovicianus</i>	Wind Cave National Park, USA	Birth	Birth	N	~0.08	+	223; 273	0 vs. 1	N	I	χ^2	7
19 Black-tailed prairie dog rats <i>Cynomys ludovicianus</i>	Wind Cave National Park, USA	Birth	LS birth	N	~0.0	=	117; 122	1 to 12+	N	I	U test	7
20 Canadian beaver <i>Castor canadensis</i>	Eastern Finland	Conception	LS birth	Y ^(a)	~2.0	-	9; 13	0 vs. 1**	N		U test	47
21 Columbian ground squirrel <i>Spermophilus columbianus</i>	Sheep River, Canada	Success	LS birth	N	~0.9	+	4; 14	R,C vs. E	Y		ANOVA	8
22 Columbian ground squirrel <i>Spermophilus columbianus</i>	Sheep River, Canada	Success	LS success	N	~1.1	+	4; 12	R,C vs. E	Y		ANOVA	8
23 Columbian ground squirrel <i>Spermophilus columbianus</i>	Dyson Creek, Canada	Success	Success	N	0.05	+	36; 10	0 vs. 1	N		G test	10
24 Columbian ground squirrel <i>Spermophilus columbianus</i>	Dyson Creek, Canada	Birth	LS success	N	N/A	+	71	1 to 6	N		Corr	9
25 Columbian ground squirrel <i>Spermophilus columbianus</i>	Dyson Creek, Canada	Success	LS success	N	0.4	+	36; 10	0 vs. 1**	N		U test	10

Table 2 continued

Population no. and species	Study location	Trait (time <i>t</i>)	Trait (time <i>t</i> + <i>t</i>)	Cost ¹	Effect size ²	D ³	N ⁴	Scale ⁵	M ⁶	C ⁷	Method used ⁸	References ⁹
14 Columbian ground squirrel <i>Spermophilus columbianus</i>	George Creek, Canada	Success	Success	N	0.05	+	25; 13	0 vs. 1	N		G test	10
15 Columbian ground squirrel <i>Spermophilus columbianus</i>	Highwood Pass, Canada	Success	LS success	N	0.1	+	25; 13	0 vs. 1**	N		U test	10
16 Columbian ground squirrel <i>Spermophilus columbianus</i>	Sheep River, Canada	Success	LS success	N	0.05	+	15; 10	0 vs. 1	N		G test	10
17 Columbian ground squirrel <i>Spermophilus columbianus</i>	Sheep River, Canada	Success	LS success	N	0.6	+	15; 10	0 vs. 1**	N		U test	10
18 Columbian ground squirrel <i>Spermophilus columbianus</i>	Turnbull National Wildlife Refuge, USA	Success	Success	N	N/A	N/A	35; 74	R,C vs. E	Y		χ^2	12
19 Deer mouse <i>Peromyscus maniculatus</i>	Kananaskis Valley, Canada	Success	LS birth	N ^(c)	0.7	-	45	0 vs. 1	N		t test	13
20 Meadow vole <i>Microtus pennsylvanicus</i>	Patuxent Wildlife Research Center, USA	Success	LS success	N	N/A	+	110	0 to 8	N		Corr	14
21 North American red squirrel <i>Tamiasciurus bairdsonicus</i>	Kluane National Park, Canada	Success	Success	N	0.10	+	39; 14	0 vs. 1 to 7	N		ANOVA	15
22 Olympic marmot <i>Marmota flaviventris</i>	Olympic National Park, USA	Success	LS success	N	1.3	+	24; 7	0 vs. 1 to 7	N		ANOVA	15
23 Richardson's ground squirrel <i>Spermophilus richardsonii</i>	Picture Butte, Canada	Success	Birth	N	~0.08	+	N/A	0 vs. 1	N	E	MCMR*	17
24 Richardson's ground squirrel <i>Spermophilus richardsonii</i>	Picture Butte, Canada	Success	Success	N	0.07	+	143; 170	Early vs. late	N	E	GLM	19
25 Alpine ibex <i>Capra ibex</i>	Belledonne-Sept-Laux Reserve, France	Success	Success	N	0.03	-	143; 170	Early vs. late	N	E	GLM	19
26 Alpine ibex <i>Capra ibex</i>	Vanoise National Park, France	Success	Success	N	~0.05	+	321; 310	0 vs. 1 to 4+	N	IE	GLMM	20
27 Bighorn sheep <i>Ovis canadensis</i>	Ram Mountain, Canada	Success	LS success	N	~0.03	+	193; 163	0 vs. 1 to 4+	N	IE	GLMM	20
28 Bighorn sheep <i>Ovis canadensis</i>	Ram Mountain, Canada	Success	Birth	Y	1.00	-	8; 6	0 vs. 1	N		N/A	48
29 Richardson's ground squirrel <i>Spermophilus richardsonii</i>	Picture Butte, Canada	Success	Success	N	0.21	+	89; 7	0 vs. 1	N		N/A	22
30 Richardson's ground squirrel <i>Spermophilus richardsonii</i>	Picture Butte, Canada	Success	LS success	N	0.20	+	N/A	1 to 13	N		Corr	22
31 Richardson's ground squirrel <i>Spermophilus richardsonii</i>	Picture Butte, Canada	Success	LS success	N	0.10	+	230	1 to 13	N		Corr	21
32 Alpine ibex <i>Capra ibex</i>	Belledonne-Sept-Laux Reserve, France	Success	Birth	N	~0.06	+	106	0 vs. 1	N	I	GLM	49
33 Alpine ibex <i>Capra ibex</i>	Vanoise National Park, France	Success	Birth	N	~0.26	+	64	0 vs. 1	N	I	GLM	49
34 Bighorn sheep <i>Ovis canadensis</i>	Ram Mountain, Canada	Success	Birth	N	~0.40	+	1027	0 vs. 1	N	IE	GLM/GEE*	24,50
35 Bighorn sheep <i>Ovis canadensis</i>	Ram Mountain, Canada	Success	Success	Y ^(c)	~0.15	-	815	0 vs. 1	N	IE	GEE*	50
36 Bighorn sheep <i>Ovis canadensis</i>	Ram Mountain, Canada	Success	Success	Y ^(f)	N/A	-	500	0 vs. 1	N	IE	GLM	24

Table 2 continued

Population no. and species	Study location	Trait (time t)	Trait (time $t + f$)	Cost ¹	Effect size ²	D ³	N ⁴	Scale ⁵	M ⁶	C ⁷	Method used ⁸	References ⁹
28 Bighorn sheep <i>Ovis canadensis</i>	Sheep River, Canada	Success	Success	N	0.09	+	155; 78	0 vs. 1	N	IE	GLM	25
29 Bison <i>Bison bison</i>	Wind Cave National Park, USA	Birth	Birth	Y ^(e)	0.77	-	7; 63	Early vs. late	N		G test	51
30 Caribou <i>Rangifer tarandus</i>	Central Arctic Herd, Alaska	Birth	Birth	Y	0.65	-	31; 18	0 vs. 1	N		N/A	52
31 Desert bighorn sheep <i>Ovis canadensis</i>	Peninsular Ranges, USA and Mexico	Success	Birth	N	N/A	N/A	68 (ID)	0 vs. 1	N		G test	53
		Success	Birth	N	N/A	N/A	68 (ID)	0 vs. 1	N		G test	53
		Success	Success	N	N/A	N/A	68 (ID)	0 vs. 1	N		G test	53
		Success	Success	Y	N/A	N/A	68 (ID)	0 vs. 1	N		G test	53
32 Elk <i>Cervus elaphus</i>	Starkey, USA	Conception	Birth	Y	N/A	-	69 (ID)	0 vs. 1	N	IE	GLM*	54
33 Moose <i>Alces alces</i>	14 populations, Sweden	Birth	Conception	N	N/A	N/A	311	0 to 2	N	IE	GLM	55
		Success	Conception	N	N/A	N/A	311	0 to 2	N	IE	GLM	55
		Birth	LS conception	N	~0.10-0.20	+	273	0 to 2	N	IE	GLM	55
		Success	LS conception	N	N/A	N/A	273	0 to 2	N	IE	GLM	55
34 Moose <i>Alces alces</i>	Many populations, Norway	Conception	Conception	N	~0.00-0.06	-	458; 57	0 vs. 1, 2	N		χ^2	56
		Conception	LS conception	N	N/A	+	196; 27	0 vs. 1, 2	N		χ^2	56
35 Moose <i>Alces alces</i>	Nelchina Basin, Alaska	Birth	Conception	Y	0.25	-	16; 47	0 vs. 1	N		t test	57
		Birth	Birth	N	0.19	-	13; 40	0 vs. 1	N		t test	57
		Success	Birth	Y	N/A	-	379	0 to 2	N	IE	GLM	26
		Birth	Success	N	0.09	-	11; 33	0 vs. 1	N		t test	57
		Birth	LS conception	N	0.22	-	10; 38	1 vs. 2	N		t test	57
		Birth	LS birth	N	N/A	+	793	1 vs. 2	N	IE	GLM	26
		Success	LS birth	Y	N/A	-	793	0 to 2	N	IE	GLM	26
36 Mountain goat <i>Oreamnos americanus</i>	Caw Ridge, Canada	Birth	Birth	Y ^(h)	~0.25-0.40	-	555	0 vs. 1	N	IE	GEE*	27,50
		Birth	Success	N	0.05	+	156	0 vs. 1	N	IE	GEE*	27,50
37 Red deer <i>Cervus elaphus</i>	Isle of Rum, Scotland	Success	Birth	Y ⁽ⁱ⁾	~0.02	-	145 (ID)	0 vs. 1	N	IE	GLM	30
		Success	Birth	N	0.21	-	370; 191	0 vs. 1	N	IE	G test	29,58,59,60
		Success	Success	N	0.11	+	245; 166	0 vs. 1	N	E	G test	29
38 Red deer <i>Cervus elaphus</i>	Many populations, Norway	Birth	Conception	N	~0.50	+	10 073	0 vs. 1	N	IE	GLM	61
39 Red deer <i>Cervus elaphus</i>	Petite Pierre National Reserve, France	Success	Conception	Y ⁽ⁱ⁾	0.27	-	395	0 vs. 1	N	IE	GLM	62
40 Reindeer <i>Rangifer tarandus</i>	Kaamanen Research Station, Finland	Birth	Birth	N	~0.03	+	N/A	0 vs. 1	N	I	MCMR/GLM*	31,63
		Success	Birth	N	~0.20	+	N/A	0 vs. 1	N	I	MCMR*	31
		Birth	Success	N	~0.01	+	N/A	0 vs. 1	N	I	MCMR*	31
		Success	Success	N	~0.15	+	N/A	0 vs. 1	N	I	MCMR*	31

Table 2 continued

Population no. and species	Study location	Trait (time t)	Trait (time $t + 1$)	Cost ¹	Effect size ²	D ³	N ⁴	Scale ⁵	M ⁶	C ⁷	Method used ⁸	References ⁹
41 Roe deer <i>Capreolus capreolus</i>	Trois-Fontaines, France	Success	Success	N	~0.08	+	476	0 vs. 1,2	N	IE	GEE*	50
42 Soay sheep <i>Ovis aries</i>	Village Bay area, Hirta Island, Scotland	Success	Birth	N	N/A	N/A	N/A	0 vs. 1,2	N	IE	GLM	33
		Success	Success	N	N/A	N/A	N/A	0 vs. 1,2	N	IE	GLM	33
		Success	LS success	N	N/A	+	N/A	0 vs. 1,2	N	IE	GLM	33
Others												
43 Antarctic fur seal <i>Arctophalax gazella</i>	Bird Island, South Georgia	Birth	Birth	Y ⁽⁶⁾	0.15	-	1188; 801	0 vs. 1	N	IE	GLM	34,35
		Success	Birth	N	N/A	N/A	N/A	0 vs. 1	N		G test	35
		Birth	Success	N	N/A	+	N/A	0 vs. 1	N	IE	GLM	34
		Success	Success	N	N/A	N/A	N/A	0 vs. 1	N		G test	35
44 Common marmoset <i>Callithrix jacchus</i>	National Zoological Park, USA	Success	Birth	Y ⁽⁰⁾	0.64	-	11; 6	1 vs. 2	N	I	χ^2	36
45 European badger <i>Meles meles</i>	Aviemore, Scotland	Birth	Birth	N	0.35	+	10; 20	0 vs. 1	N		Fisher test	64
46 European badger <i>Meles meles</i>	Myrtham Woods, UK	Birth	Birth	N	N/A	+	N/A	0 vs. 1	N		χ^2	37
47 Fur seal <i>Arctophalax tropicalis</i>	Amsterdam Island, Indian Ocean	Birth	Birth	N	~0.12	+	238 (ID)	0 vs. 1	N	IE	MCMR*	38
		Success	Birth	N	~0.09	+	238 (ID)	0 vs. 1	N	IE	MCMR*	38
		Birth	Success	N	~0.00	=	238 (ID)	0 vs. 1	N	IE	MCMR*	38
		Success	Success	N	~0.12	+	238 (ID)	0 vs. 1	N	IE	MCMR*	38
48 Grey seal <i>Halichoerus grypus</i>	North Rona, Scotland	Birth	Birth	N	N/A	+	91 (ID)	0 vs. 1	N		G test	65
		Success	Birth	N	N/A	N/A	91 (ID)	0 vs. 1	N		G test	65
		Birth	Success	N	N/A	N/A	91 (ID)	0 vs. 1	N		G test	65
		Success	Success	N	N/A	N/A	91 (ID)	0 vs. 1	N		G test	65
49 Japanese macaque <i>Macaca fuscata</i>	Kinkazan Island, Japan	Success	Conception	Y	0.69	-	19; 58	0 vs. 1	N		χ^2	66
		Birth	Birth	Y	0.57	-	35; 66	0 vs. 1	N		N/A	66
		Success	Birth	Y	0.44	-	29; 9	0 vs. 1	N		N/A	66
50 Mountains hare <i>Lepus timidus</i>	Corgarff, Scotland	Conception	LS conception	Y	0.5-0.7	-	27 (ID)	0 to 4	N	I	LM	67

Table 2 *continued*

Population no. and species	Study location	Trait (time <i>t</i>)	Trait (time <i>t</i> + 1)	Cost ¹	Effect size ²	D ³	N ⁴	Scale ⁵	M ⁶	C ⁷	Method used ⁸	References ⁹
51 Weddell seal <i>Leptonychotes weddellii</i>	Erebus Bay, Antarctica	Birth	Birth	Y ^(f)	0.21	–	607 (ID)	0 vs. 1	N	IE	MCMR*	41
52 Weddell seal <i>Leptonychotes weddellii</i>	Vestfold Hills, Antarctica	Birth	Birth	N	N/A	N/A	1368 (ID)	0 vs. 1	N	E	MCMR*	42
53 Wolverine <i>Gulo gulo</i>	Sarek National Park, Sweden	Birth	Birth	Y ^(a)	0.32	–	31; 17	0 vs. 1	N		χ^2	68
		Success	Success	Y	0.45	–	21; 14	0 vs. 1	N		Fisher test	68
		Birth	LS success	N	0.3	–	6; 17	0 vs. 1	N		U test	68
		Success	LS success	Y	0.8	–	25; 17	0 vs. 1	N		Corr	68

Notes: See Notes of Table 1 for details on how the literature review was performed. N/A, information not available or data not in a comparable format.

¹Y, costs of reproduction reported; N, no cost reported; (a), only a tendency; (b), stronger effect for females with greater reproductive effort; (c), only compared primiparous at 2 vs. 3 years old; (d), only compare young vs. old primiparous; (e), costs only for low-quality females; (f), stronger effect at high density and in lighter females; (g), costs only for early primiparous females; (h), costs only in young females (and effect stronger for primiparous females), at high density, and for low-quality females at low density; (i), stronger effect for young and old females; (j), costs only for primiparous females; (k), stronger effect for primiparous females, but no effect of age at primiparity; (l), costs only in small females.

²Effect sizes that were estimated from figures or from different categories (see Notes) are marked with ‘~’.

³D, direction of the effect.

⁴N, sample size in terms of female-events; ID, the number of female-events was not available, so the sample size provided represents the number of females included in the study. When available, sample size was separated in different female categories and presented in the following order: reproductive vs. non-reproductive females, or females with large vs. small litter size.

⁵Scale on which the effect size is based upon, where numbers represent the number of offspring, R, reduced litter; C, controlled litter; E, enlarged litter; Early, early first time breeders; Late, late first time breeders; **no effect of different litter size on future reproduction.

⁶M, experimental manipulation of reproductive effort; Y, yes; N, no.

⁷C, (co)variables included in the analyses; I, study accounted for variable(s) relating to individual quality; E, study accounted for variable(s) relating to environmental conditions.

⁸LM, linear model; GLM, generalized linear mixed model; GEE, generalized estimating equations model; MCMR, multivariate capture-mark-recapture model; ANOVA, analysis of variance model; Corr, correlation; *studies that used an information-theoretic approach (e.g. Akaike Information Criterion).

⁹References are provided in Appendix S3.

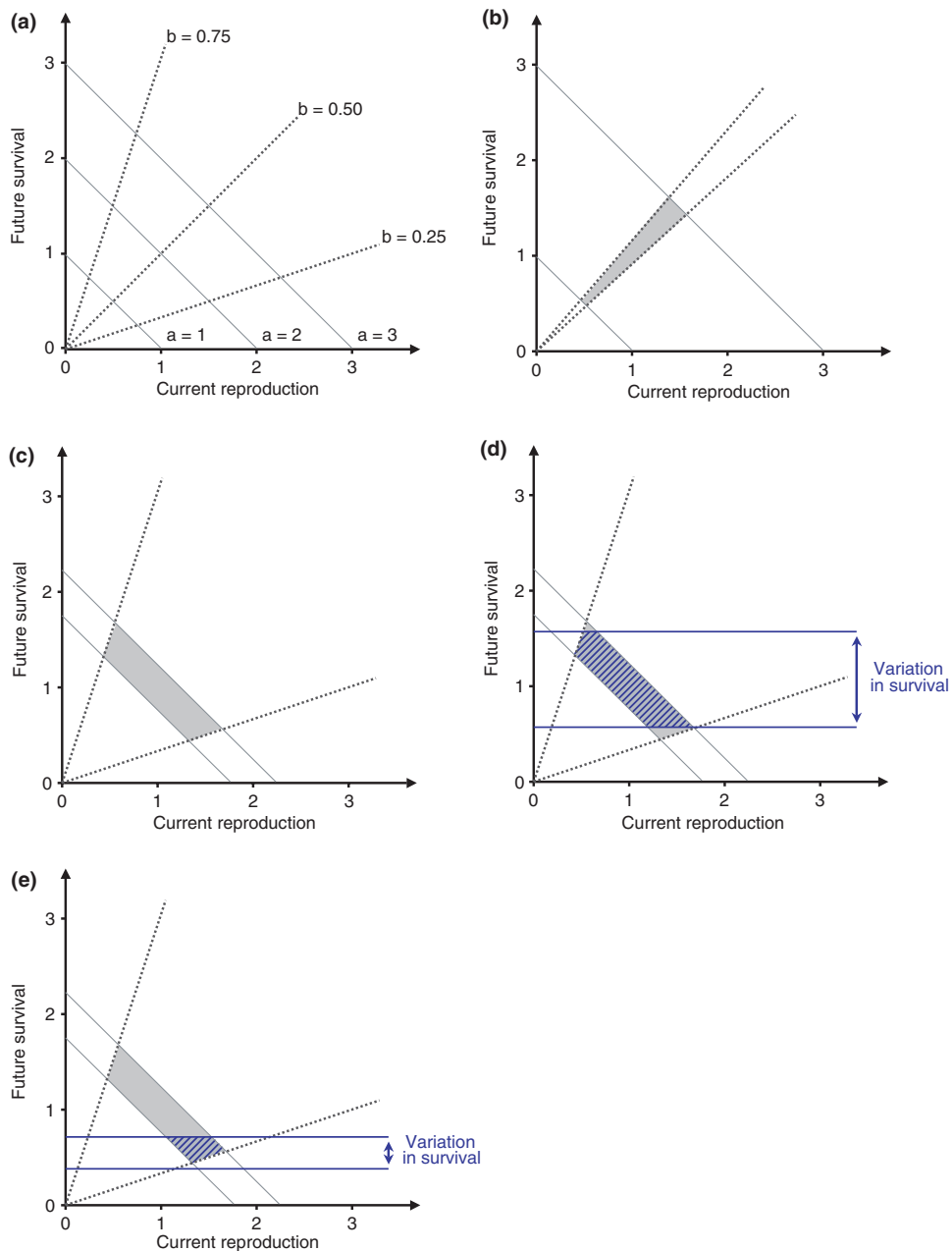


Figure 1 (A–C) The van Noordwijk and de Jong model, explaining positive and negative correlations observed among life-history traits, according to variance in resource acquisition and allocation (reproduced from van Noordwijk & de Jong 1986). (A) The total amount of resources available (i.e. acquisition; ‘a’) in relation with the relative resource allocation (‘b’) between two life-history traits, here current reproduction and future survival. (B) The relative variation in resource acquisition (a) among individuals of a population is large and the relative variation in resource allocation (b) is small, such that the two traits are positively correlated (observations lie in the grey zone). (C) The opposite case, showing negative correlations between current reproduction and future survival, i.e. costs of reproduction. (D, E) The van Noordwijk and de Jong model in a situation where we should observe costs of reproduction (i.e. C) for which we added the influence of variance in fitness components (blue lines). (D) A case where survival has a high variance and most of the potential for observing costs of reproduction is encompassed (observations now lie in the blue zone). (E) A case where survival has a low variance and observations (lying in the blue zone) show no relationship between current reproduction and survival.

allocation curves according to the life-history strategy of each group to better portray these species. As ungulates have a conservative reproductive tactic favouring survival over current reproduction, we drew the curves representing variance in allocation closer to future survival than to current reproduction (Fig. 2a). Because ungulates should not favour current or future reproduction (at least during their prime-age stage when survival is close to 1; Gaillard *et al.* 2000), we placed the allocation curves symmetrically for these two traits (Fig. 2b). In contrast, rodents have a faster life-history strategy, so that allocation in current reproduction should generally be greater than allocation in both future reproduction and survival. We thus drew the

allocation curves closer to current reproduction in both cases (Fig. 2c,d). To these curves, displaying the responses of fitness components to current reproduction over the whole range of possible values, we added curves representing the variance in fitness components for both groups (based on Gaillard & Yoccoz 2003). Again, the exact locations of the curves are not that important, but the distance between the curves, representing the variance of the trait, is fundamental because it influences the range of observed values (e.g. blue zones). When the variance is low (Fig. 2a,d), the blue zone representing the values observed for a particular life-history strategy is small and it is difficult to detect a relationship between the two fitness compo-

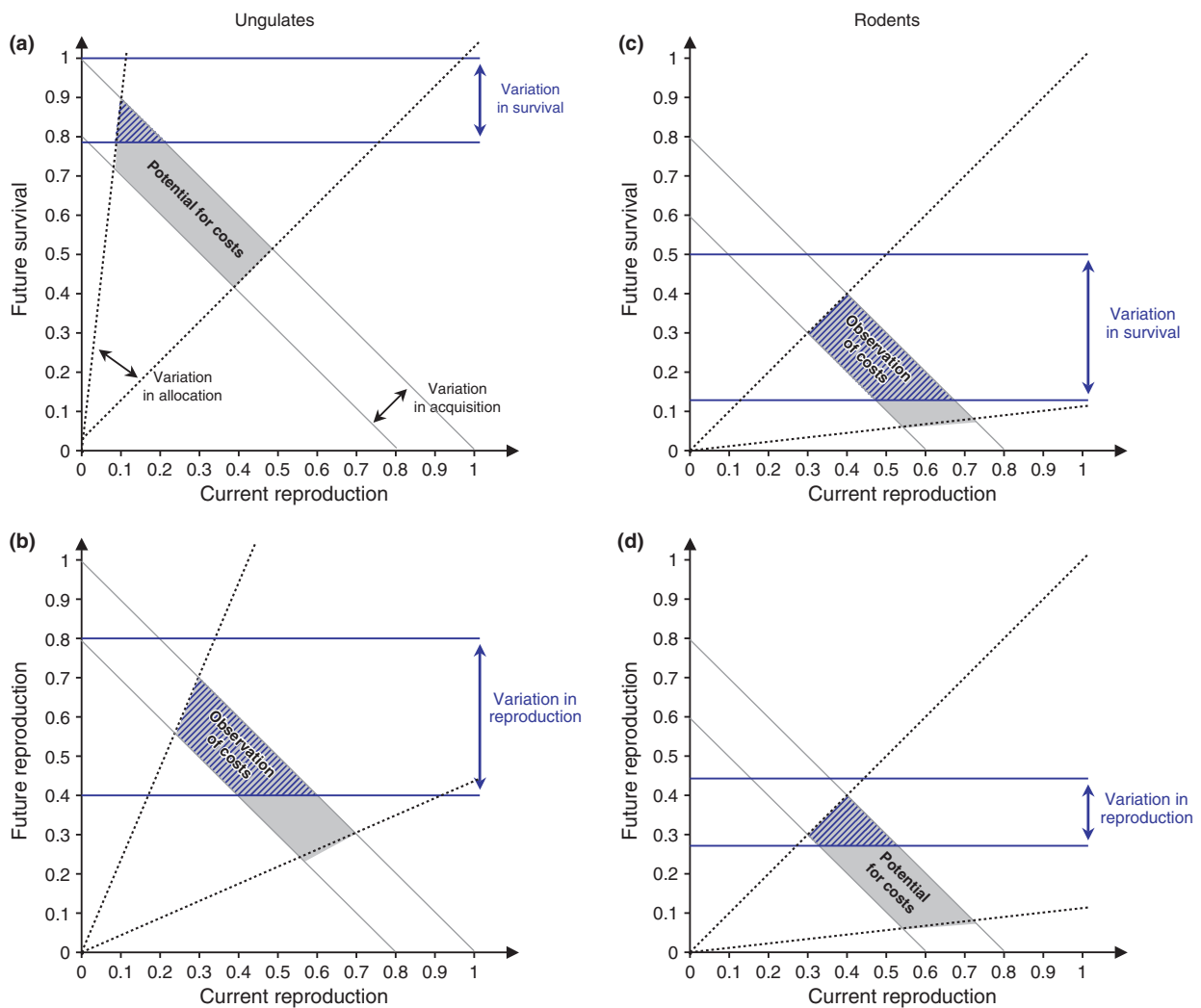


Figure 2 Relative investment in current reproduction vs. survival (top panels) and future reproduction (bottom panels) in relation with variation in resource allocation and acquisition (black arrows; from van Noordwijk & de Jong 1986, see Fig. 1) and with variation in the fitness trait studied (blue arrows, this study), for ungulates (left panels) and rodents (right panels). The grey zones represent the potential for observing costs of reproduction when accounting for variation in resource allocation and acquisition, whereas the blue zones represent the areas where we should observe costs of reproduction after accounting for variance in the fitness component.

nents, as demonstrated in Fig. 1E. Conversely, when the variance is high (Fig. 2b,c), the range of observed values is wide and the potential for detecting costs of reproduction is large. Thus, the expected negative correlation between the two traits can be quite easily detected.

Therefore, our evolutionary model demonstrates that detecting costs of reproduction for a given fitness component does change as a function of the variance of this component. As the speed of the life-history strategy is clearly related to the variance of traits (Pfister 1998; Gaillard *et al.* 2000; Morris & Doak 2004), we can hypothesize that 'the fitness component most sensitive to costs of reproduction should differ depending on the life speed of the focal species'. Accordingly, we predict that costs of reproduction should mainly be reported in terms of future reproduction in ungulates and in terms of future survival in rodents (Fig. 2). We therefore expected to find relatively more studies reporting survival costs of reproduction in rodents than in ungulates, and relatively more studies reporting costs of reproduction in terms of future reproduction in ungulates than in rodents.

REVIEW OF THE LITERATURE AND TESTING OUR EVOLUTIONARY MODEL

Overall, we identified 153 studies assessing fitness costs of reproduction in wild mammals, i.e. excluding studies on domesticated species and humans. Mammalian species studied in these papers included mainly rodents and ungulates, and to a lesser extent pinnipeds and primates. Most studies assessed direct costs of reproduction in females in terms of survival ($n = 38$ populations, 42 studies; Table 1) and future reproduction ($n = 53$ populations, 55 studies; Table 2). We therefore focused our review and tested our evolutionary model based on these studies (but see Appendix S2 for a synthesis of results on costs of reproduction in males, costs of first reproduction, cumulative costs of reproduction, and indirect costs of reproduction).

For each study, we compiled costs of reproduction reported according to different categories. First, we separated costs in terms of future survival (Table 1) from costs in terms of future reproduction (Table 2). For future reproduction, we further separated costs into six categories according to the trait and the stage at which reproduction was assessed: conception rate, litter size at conception, parturition rate, litter size at parturition, weaning success, and litter size at weaning. For both survival and reproductive costs of current reproduction, we distinguished whether the occurrence of a cost was tested in relation to current conception, parturition, or weaning success. To assess the influence of current litter size, we presented effect sizes for the influence of current reproduction on future traits scaled

on litter sizes, e.g. reporting effect size between a litter size of 0 vs. 1 or among various litter sizes (e.g. from 1 to 13) depending on the study design (see 'scale' column in Tables 1 and 2). For the conception stage, we included studies for which the reproductive status of females was assessed from shortly after mating to prior to late gestation. For studies in which the reproductive effort was manipulated by adding or removing offspring after parturition, we classified effects of the manipulation on future reproduction and survival as costs associated with weaning success because the manipulation only influenced the females' allocation to lactation. For each cost of reproduction test, we reported the occurrence along with the effect size, the direction of the effect, the sample size and the statistical method used, and whether individual and environmental covariates were taken into account (Tables 1 and 2).

To test our evolutionary model that 'the most sensitive fitness component of future performance to current reproduction varies with life speed', we compiled studies that reported costs of reproduction in terms of future survival or reproduction, for both rodents and ungulates. We considered costs of reproduction to have occurred in a population when a cost was reported in at least one reproductive stage, and we separated the responses of future survival and future reproduction (see Tables 1 and 2). The empirical evidence we obtained supported our evolutionary model. We found a greater proportion of populations showing evidence of costs of reproduction in terms of future reproduction in long-lived ungulates (50% – 9 populations of 18) than in short-lived rodents (21% – 5 of 24; Table 2). Furthermore, although there were few studies on survival costs of reproduction in ungulates, we also found a greater proportion of populations demonstrating costs in terms of survival in rodents (41% – 9 of 22) than in ungulates (29% – 2 of 7; Table 1). While the absolute proportion of studies reporting costs of reproduction might over-estimate the true frequency of costs of reproduction because negative results are usually less likely to be published than positive ones (the so-called publication bias or 'file drawer' problem, Rosenthal 1979), the relative proportion among traits and life speed should not be influenced. Therefore, the variance observed in a given fitness component seems to have a fundamental influence on the response of that component to current reproduction.

As mentioned previously, the variance observed in fitness components is the result of both a statistical and a biological influence. The statistical detection of a cost of reproduction for a trait presenting a high mean, and hence low variance, will be more difficult than for a trait presenting a mean close to 0.5. In our review, we compared rodents and ungulates, and ungulates typically have higher survival. Hence, a doubling in mortality as a result of costs of reproduction

could lead for example to a reduction in survival in the order of 0.80 to 0.60 for rodents and 0.95 to 0.90 for ungulates. Although costs of reproduction double mortality in both cases, the latter will be harder to detect statistically. Nevertheless, the variance observed in fitness components is also constrained biologically as a result of environmental canalization (Stearns *et al.* 1995) because the inverse relationship between the potential impact of a trait on fitness and the variance of that trait holds after differences in mean trait values are accounted for (Gaillard & Yoccoz 2003). Therefore, the selection against environmental variability observed in traits having a high potential impact on fitness (i.e. high elasticity) is likely to account for the observed variation in patterns of costs of reproduction among species and traits. We thus propose that environmental canalization plays a key role in shaping the evolution of costs of reproduction.

DIFFICULTIES IN ASSESSING COSTS OF REPRODUCTION EMPIRICALLY

Influence of energetic allocation during the reproductive life cycle

We have demonstrated in the previous sections that detection of costs of current reproduction should depend on the variance of fitness components affected by current reproduction. Nevertheless, current reproduction is not an instantaneous and simple process, but rather spans a time period and involves several successive stages in mammals (Gittleman & Thompson 1988). Indeed, females first come in oestrus and conceive during the mating period. Mating is a relatively short period followed by a longer gestation period that ends when pregnant females give birth – the parturition stage. Females will then lactate until they wean their offspring. This stage is sometimes followed by a post-weaning allocation period or by a maternal recovery phase before the next oestrus. Each of these stages has evolved through specific selection pressures, from which originated diverse life-history strategies in mammals.

Overall, as the reproductive cycle progresses, the total energetic allocation will increase from the accumulation of stage-specific energetic allocation. In addition, energetic allocation to reproduction generally increases throughout the stages of the reproductive life cycle, so that energetic allocation during conception is lower than during early gestation, both being lower than during late gestation and early lactation (Sadleir 1984; Gittleman & Thompson 1988). Therefore, the stage at time t used to compare the future performance between reproductive and non-reproductive females could influence the probability of detecting costs of reproduction. Costs of reproduction, however, were less frequently reported in relation to weaning success (28% – 16

populations of 57) than parturition (41% – 24 of 58; Tables 1 and 2). Although costs of reproduction associated with conception were more frequent (75% – 3 of 4), too few studies assessed the influence of this reproductive stage to provide a reliable comparison with other reproductive stages. We found similar results when we calculated these proportions separately for future survival and future reproduction for rodents and ungulates, with the exception of costs in terms of future reproduction in ungulates for which the proportions were similar for parturition and weaning success (Fig. 3).

That costs of reproduction associated with lactation are not more important than those for gestation could be the result of an increase in the average quality of reproductive females throughout the reproductive life cycle. Indeed, lower quality females are more likely to abort than females in better condition (Cameron *et al.* 1993; Tveraa *et al.* 2003), which are also more likely to raise an offspring to weaning (Weladji *et al.* 2006; Hamel *et al.* 2009b). Therefore, the average quality of reproductive females is likely greater at weaning than at conception, potentially making it more difficult to detect costs of reproduction at a late stage of the reproductive cycle. Another, non-exclusive explanation for this unexpected result is that the energetic allocation to gestation is more important than what has been previously assumed (Sadleir 1984; Gittleman & Thompson 1988). Interestingly, many populations included in our study live in temperate environments, where gestation often occurs in

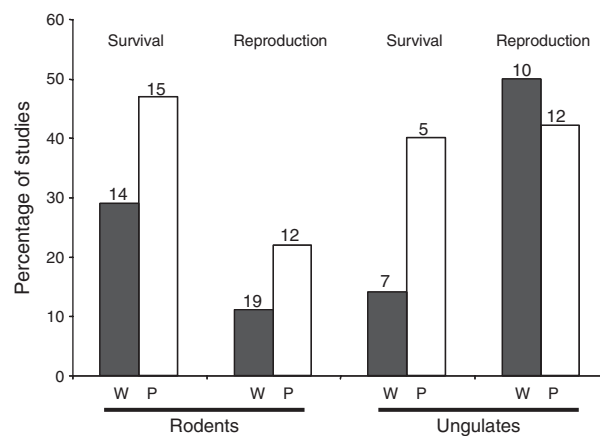


Figure 3 Percentage of studies reporting costs of reproduction in terms of future survival or reproduction as a result of weaning success (W) and parturition (P), for rodents and ungulates. Costs of current reproduction at different life stages were sometimes tested using more than one trait measuring future reproduction (see Table 2), so we considered costs of reproduction to have occurred at a specific reproductive stage when a cost was reported at least once within a population for that life stage. Numbers above the bars refer to the number of populations for each category.

winter or early spring, a time when resources are more limiting than when females are lactating in summer. The plasticity for compensating for energetic allocation may therefore be more important during lactation than during gestation. So, even if gestation may require less absolute energy than lactation, it may necessitate a high energetic allocation relative to available resources. It is also possible that early reproductive stages might be associated with costlier behaviours (e.g. behaviours increasing vulnerability to predation) than later ones. Alternatively, there could be a bias originating from the misclassification of the reproductive status of females. Indeed, offspring mortality can be important during early lactation (see Gaillard *et al.* 2000 for a review on ungulates), making it difficult to distinguish if a female lost offspring shortly after birth or if she did not give birth (even when reproductive status is determined shortly after birth). As the energetic costs of gestation are greatest during the last third of gestation and those of lactation highest in early lactation (Sadleir 1984; Maugé *et al.* 1999), the potential misclassification of female reproductive status could result in an underestimation of costs of reproduction associated with weaning success and an overestimation of parturition costs.

Confounding variables and statistical issues

Estimating fitness costs of reproduction means measuring the causal effect of varying allocation to reproduction on future survival and reproduction (referred to as response traits). Reznick (1985, 1992) listed four approaches for estimating costs of reproduction: (1) phenotypic/observational relationships between reproductive allocation and response traits, (2) manipulations of reproductive allocation, (3) genetic correlations among reproduction and survival and (4) selection experiments measuring the response to changes in allocation. The latter two approaches have rarely been used in wild mammals because of the difficulties associated with obtaining reliable estimates of genetic correlations or conducting selection experiments in the wild (but see for example Nussey *et al.* 2008). Therefore, we will focus on the first two, emphasizing environmental and individual heterogeneity, and difference in terms of response traits and linearity of effects.

First, estimations of costs of reproduction must be based on unbiased estimates of response traits, an endeavour that often implies advanced statistical modelling. The main issue with wild mammals, as with other organisms, is detection probability – individuals may for example be alive but are not captured, or have dispersed from the study area. Only in a few cases can we safely assume that detectability is 1 (e.g. populations in artificial settings, Oksanen *et al.* 2001; Weladji *et al.* 2008, or on island, Moyes *et al.* 2006). Ignoring detection probabilities of less than 1 can lead to important

biases (Gimenez *et al.* 2008). Other problems, such as separating dispersal from survival (Boulinier *et al.* 1997), can be hard to solve without specific field designs and statistical analyses.

Estimating causal effects of differences in allocation using observational data is difficult because of confounding variables (Fig. 4a). Causality and confounding variables are difficult concepts in science that are strongly related in the statistical literature to the distinction made between experimental and observational studies (Greenland & Morgenstern 2001). Ideally, one would like to observe the same individual at the same time/age/location with different levels of reproductive allocation, and then measure the response traits. Of course, this is not possible in practice and therefore we measure different individuals that will differ in reproductive allocation, but also in other variables, so-called confounders. Total acquisition is a typical confounder (Fig. 4a–c). These confounders might affect reproductive allocation, response traits, or both, but these effects can be minimized by using specific designs and analytical methods. The preferred design is based on randomization, with different levels of allocation being randomly assigned to different individuals. If randomization is used, individuals providing different allocations as a result of experimental manipulation – e.g. adding/removing young in a litter – are not expected in a statistical sense (i.e. on average) to differ in terms of confounders. Therefore, in the case of a linear response, we expect randomization to remove any bias (Fig. 4d), and thus it is the preferred approach to get unbiased estimates. Concerns with experimental manipulations are related to variation of reproductive allocation outside the natural range and to the interaction of reproductive allocation with individual characteristics such as the initial reproductive allocation (Fig. 4e). An alternative to randomization is a design based on matching (e.g. grouping individuals that are similar with respect to confounders), an approach frequently used in epidemiology (Greenland & Morgenstern 2001). Analytical methods can also be used, but they will rather focus on incorporating confounders as covariates in the statistical modelling process. Both matching and analytical methods will only be successful if we are able to choose the right confounders. Trying to correct for bias using a statistical approach will give accurate answers only if the path and linearity of the effects are correctly modelled, since assuming a wrong causal model can increase or decrease the confounding bias (McNamee 2003). If heterogeneity can be measured and therefore controlled for, costs of reproduction can be estimated accurately (see Table 3a for a summary of covariates used in studies reviewed here). To summarize, there are trade-offs between removing bias based on the design – i.e. manipulation and randomization – and controlling for it through the use of confounders in

statistical models. The former is usually restricted to small species (e.g. rodents) or populations in semi-artificial settings, and manipulations often imply unnatural conditions, such as fostering unrelated offspring. The latter, if based on high-quality longitudinal studies, is likely to provide accurate estimates of costs [e.g. Tavecchia *et al.* (2005) found similar estimates when comparing costs based on experimental and observational studies].

If ignored, individual heterogeneity in allocation and acquisition can also affect estimates of costs of reproduction in at least two cases: if there is a systematic relationship between allocation and acquisition (Fig. 4e), and if the response traits are non-linearly related to variation in allocation (Fig. 4f). The latter case is particularly relevant when response traits are proportions, and thereby con-

strained between 0 and 1, which is typical for studies on fitness costs of reproduction. Models such as logistic regression will assume some form of sigmoid relationship, and averaging non-linear responses will lead to a different response than the within-individual responses (Carlin *et al.* 2001; Fig. 4f). Random effect models (e.g. generalized linear mixed models; GLMM) can control for this heterogeneity and remove this source of bias, and their use has increased in recent years (van de Pol & Verhulst 2006; Tables 1 and 2).

Another source of potential bias is associated with temporal changes in acquisition and thereby in response traits – large multiannual density fluctuations and seasonality being the foremost examples for small, multivoltine species such as voles (e.g. Lambin & Yoccoz 2001). Total

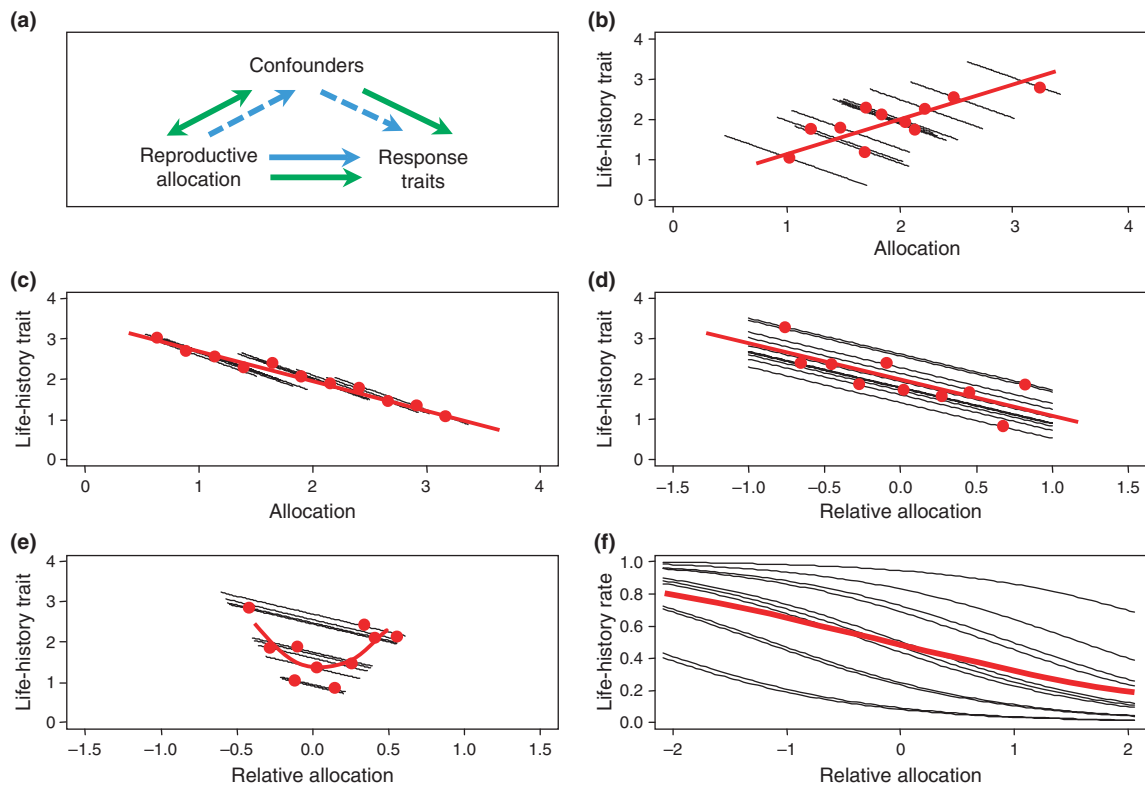


Figure 4 (a) Confounders are often defined as variables correlated to the allocation and affecting the response traits (continuous arrows). Proper confounders are variables such as home range or territory quality of an individual (green arrows): they are correlated with the allocation (where the *correlation* is represented by the double-direction arrow) and also influence survival and reproduction. However, variables such as individual body mass measured during the allocation period (blue arrows) are directly affected by the allocation (where the *causation* is represented by a single-direction arrow). In the latter case, such variables represent indirect effects on the response (dotted arrows) and are not confounders. Therefore, knowledge of the direction of effects is necessary to get unbiased estimate of the total effect of allocation on response traits. (b) If individuals (represented by thin continuous lines, dots show the unique observation that can be made) vary a lot in their total acquisition, the observed relationship between allocation and the response trait (red dots) is severely biased. (c) If individuals vary mainly with respect to allocation, this bias is negligible. (d) In an experimental setting, individuals have on average the same variation in allocation, and the slope of the mean response will be identical to the individual slopes. (e) If variation in allocation shows a systematic relationship with the response trait, the mean response can wrongly show non-linear patterns. (f) If the relationship between allocation and the response trait is non-linear, the average response will differ from the individual responses.

Table 3 Summary of the number of populations included in our review on costs of reproduction in mammalian populations (a) according to the type of approach used (experimental vs. observational) and the covariates included, and (b) providing estimates of effect size or enough information to estimate it, vs. providing only test statistics. When a population could be included in two categories, we counted only 0.5 in each category. Numbers in parenthesis represent the summary of the number of populations including covariates for populations that used an experimental approach only

	Approach		Covariates included			
	Experimental	Observational	None	Environmental [E]	Individual [I]	E + I
(a) Survival costs						
Rodents	6	16	11 (3)	3 (1)	3 (1)	5 (1)
Ungulates	0.5	6.5	2	0	1	4
Others	0	9	2	2	2	3
Total	6.5	31.5	15 (3)	5 (1)	6 (1)	12 (1)
Reproductive costs						
Rodents	8	16	14 (3)	4.5 (3)	3 (2)	2.5 (0)
Ungulates	0	18	4.5	0	3	10.5
Others	0	11	5.5	1	2	2.5
Total	8	45	24 (3)	5.5 (3)	8 (2)	15.5 (0)
(b) Survival costs						
	Before 2000			2000 until now		
	Not available	Can be estimated	Estimates provided	Not available	Can be estimated	Estimates provided
Rodents	3	3.5	7.5	1	3	4
Ungulates	1	1	1	1	0.5	2.5
Others	2	0	2	0	0	5
Total	6	4.5	10.5	2	3.5	11.5
Reproductive costs						
Rodents	4.5	5	6.5	3	2	3
Ungulates	2.5	1.5	4	2.5	6	1.5
Others	2.5	0	3.5	1	1	3
Total	9.5	6.5	14	6.5	9	7.5

acquisition will depend on resource availability, which varies tremendously between and within years. Hence, costs of reproduction vary among years and generations within a year, making it challenging to accurately describe the relationship(s) between allocation and response traits. Snowshoe hares (*Lepus americanus*), for example, are characterized by high adult survival and high reproductive output in the increase phase, whereas hares born in the decline phase have low reproductive output and die rapidly from predation (Stefan & Krebs 2001; Sheriff *et al.* 2009). This is a good example of systematic differences in allocation that cannot be used to assess costs of reproduction (see also Ruf *et al.* 2006). Such differences in allocation are likely due to changes in predation risk and stress, which also affect future survival since they are temporally auto-correlated.

In our review, we found that studies controlling for individual and/or environmental heterogeneity tended to report evidence of costs of reproduction more often than those that did not (47% – 25/53 populations vs. 29% –

11/38 populations; Tables 1 and 2). This is expected since confounders are likely to mask costs of reproduction (Fig. 4b) or to decrease precision in experimental studies.

Estimating costs of reproduction has been less often a focus than finding statistical evidence for their existence, which usually is done based on *P*-values (e.g. Reznick 1985). However, Table 3b shows that most studies provided enough information to reliably estimate an effect size. Note that there was no clear temporal trend with respect to publication year and the type of information provided. This overemphasis on statistical significance can bias comparisons among studies because *P*-values are affected by a variety of factors, such as sample size and the type of response traits (Yoccoz 1991). For example, sample size in Table 2 varied between *c.* 20 and 10 000, which in terms of a standard error of a regression coefficient means a factor of over 20, and corresponding effects on *P*-values. Response traits such as survival or reproductive rates also result in less precise regression coefficients compared with traits such as

offspring body size for example, because they often rely upon more complex models (e.g. capture-recapture models) and have distributions with high variance (e.g. binomial). P -values can also be influenced by the extent of variation in reproductive allocation, which can vary systematically among species: litter size cannot be changed much in large mammals, being 1 or 2 in most species (Hayssen *et al.* 1993), while small mammals or even middle-sized mammals like the Arctic fox (*Vulpes lagopus*) can have a litter size of up to 18 (A. Angerbjörn, unpublished data). Similar problems exist when using R^2 as a measure of effect size. Therefore, there is a need for consistent metrics of costs of reproduction among species, response traits, and measures of reproductive allocation. A cost of reproduction usually corresponds to a regression coefficient, which is a rate with one scale for the allocation (the predictor) and one scale for the response. Scales or units can refer either to absolute values (e.g. energetic requirements associated with different litter sizes) or relative, standardized values. Standardization is often done by using the standard deviation (SD; e.g. litter size/SD[litter size] as a measure of allocation), but this is valid only if SD is a reliable measure of relative variation. Finally, one could standardize the response traits so that they are measured on a scale representing similar impacts on fitness. Similar issues focusing on scaling have also been raised for other related questions, such as for assessing the importance of demographic parameters for fitness variation (Link & Doherty 2002; Gaillard & Yoccoz 2003) or the impact of climatic conditions on individual survival (Grosbois *et al.* 2008). More work is needed to develop comparable measures of costs, and the absence of a clear scale for measuring costs likely accounts for the lack of estimates in many studies.

WHAT HAVE WE LEARNED AND WHERE SHOULD WE GO FROM NOW?

To explain variation in the occurrence of costs of reproduction among species and fitness components, we proposed to incorporate variance in fitness components to the model of resource acquisition and allocation proposed by van Noordwijk & de Jong (1986). The empirical evidence reviewed supported our evolutionary model, demonstrating that the chance of detecting a cost of reproduction is lower when the fitness component studied has a low compared with a high variance. This suggests that the fitness component being most affected by costs of reproduction varies with life speed. As low variance in fitness components likely results from environmental canalization (Stearns *et al.* 1995; Gaillard & Yoccoz 2003), our model indicates that selection against environmental variability plays a key role in shaping the evolution of costs of reproduction. Because costs of reproduction can

markedly influence population dynamics (Silvertown & Dodd 1999; Proaktor *et al.* 2008), our study suggests that environmental canalization can have not only direct but also indirect demographic consequences on population growth. By extending a well-known life-history model, our work provides a further contribution to a better understanding of life-history variation that should be relevant to all evolutionary ecologists interested in life-history trade-offs. Indeed, although our review focused on mammals, the model we proposed is expected to apply to any species. Further studies, however, will be required to test this. Our model will also allow several new evolutionary hypotheses to be evaluated. For example, as survival and reproduction in sexually dimorphic and polygynous species are more variable in males than in females (see e.g. Clutton-Brock *et al.* 1982), we should expect to observe costs of reproduction more often in males than in females. However, even if costs of reproduction should have a strong influence on the evolution of life-history strategies in mammalian males, we still have a poor knowledge of this due to the scarcity of studies on costs of reproduction in males (see Appendix S2). Finally, we highlighted important issues regarding estimations of costs of reproduction. We hope this will encourage the development of statistical methods and that it will trigger awareness in accounting for these issues when studying costs of reproduction.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 How should costs of reproduction be measured?

Appendix S2 Other costs of reproduction.

Appendix S3 References listed in Tables 1 and 2.

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